

The

EXTENDED
ORGANISM

*The Physiology of
Animal-Built Structures*

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Preface

This is a book about structures built by animals—sort of. I actually wish to explore an idea: that the edifices constructed by animals are properly external organs of physiology.

The subject of animal-built structures has traditionally been dominated by students of animal behavior and evolutionary biology. Consider the following. A collection of classic papers on animal architecture, *External Construction by Animals* (1976), compiled by Nicholas and Elsie Collias, is part of a series entitled *Benchmark Papers in Animal Behavior*. The authoritative work on the subject, *Animal Architecture* (1974), was written by Karl von Frisch, the Nobel Prize–winning behavioral biologist. A more recent book, by Michael Hansell, is entitled *Animal Architecture and Building Behavior* (1984): the title makes the point. Students of evolution, for their part, have long valued the fossilized remnants of animal-built structures as probes into the past, a view reflected in such books as S. K. Donovan’s *Paleobiology of Trace Fossils* (1994) and Richard Crimes’s *Trace Fossils: Biology and Taphonomy* (1990). Finally, of course, there is Richard Dawkins’s eloquent book, *The Extended Phenotype* (1982).

For the most part, these treatments have been utilitarian in their approach to this subject—animal-built structures as examples of “frozen behavior,” tools to probe the past, devices that genes use to project their influence beyond the organism’s skin. I felt that a treatment of how these structures function for the animals that build them was lacking, and since I am a physiologist, I decided to try to fill the breach.

I have tried to make the book appealing to a broad audience. I hope students of animal behavior will enjoy a functional analysis of how such structures work. I hope physiologists will enjoy seeing the novel ways physiology can be applied to something besides organisms and cells. I hope evolutionary biologists will appreciate seeing the functional “flesh and bones” of the extended phenotype. Finally, I hope ecologists will enjoy delving into their discipline’s historical roots as a physiological science.

Writing for breadth can be hazardous, though, for it is impossible to anticipate every reader’s needs. Some passages may cover ground already familiar to some readers, but I hope all will find something new of interest. I have not shied away from quantitative and mathematical analyses, but all are straightforward and none require advanced training. I have used as many concrete examples as possible, but I have had to be very careful in making my selections: the hardest part of writing the book was in deciding what to leave out. I know many will wonder why I have left out their “favorite” structures—if so, please let me hear from you, just in case there is a second edition. For reasons more of personal interest than anything else, I have focused on invertebrates, so structures like birds’ nests or beaver lodges have not been considered.

During the conception and writing of this book, I have been the beneficiary of numerous acts of generosity and good will. My editor at Harvard University Press, Ann Downer-Hazell, has been extraordinarily patient in helping me resolve difficult issues of style

and presentation. She took a chance with me, an untested author, and I hope she now feels the gamble was worth it. Kate Schmit brought art and style to the final copy-editing, taking innumerable sentences and paragraphs that I thought I had tortured into a semblance of respectability and, with a brush and a flair, making them elegant. Three anonymous reviewers of earlier drafts of this book provided many thoughtful, perceptive, and critical comments. I hope they agree that they helped me make the book better. Bill Shields, my colleague at the SUNY College of Environmental Science and Forestry has been invaluable in challenging, openly, honestly and joyfully, some of my stranger thoughts—he is, in short, a *mensch*. Jim Nakas has been

my resident expert on Greek and Latin etymology and phraseology. I have enjoyed talking with Charlie Hall about Howard Odum and maximum power. Earth-Watch, a remarkable organization, has been steadfast in supporting my work on termites; it was this work that got me thinking seriously about animal-built structures. The Trustees of the State University of New York generously granted me a sabbatical leave, which gave me the time I needed to complete writing the book. Finally, my wife Debbie and my two girls, Jackie and Emma, have had to put up with a husband and father who, while present physically, was often absent mentally. Their unwavering support and faith in me is more valuable to me than I can ever hope to express.

CHAPTER ONE

The Organism's Fuzzy Boundary

The building of structures by animals is widespread, ubiquitous even. Sometimes these structures are humble: simple tunnels in the ground or small piles of rubble. Sometimes they are grand—the nests built by some species of termites to house their colonies are, in their own way, magnificent, even sublime. Sometimes they are built unintentionally—the tracks left by an animal passing over or through sand or mud, for example. Sometimes they are built with seeming intention, like the “fog catchment trenches” the Namib desert beetle *Lepidochora* uses to capture water wafted inland from the Atlantic by coastal fogs. An animal-built structure may be ephemeral, disappearing with the next tide or gust of vigorous wind, or it may be relatively permanent, solidified by mucus or reinforced with silken threads. Some edifices are the work of masons, made from grains of sand laboriously glued together one after another. Others are the work of sculptors, like the holes carved from sandstone by sea urchins. Others still are the work of miners, like the tunnels dug into trees by bark beetles, or of weavers, like the woven nests of birds or the webs of spiders. Sometimes the workmanship seems sloppy, as in the rather haphazard piles of logs and twigs in a beaver's lodge, but occasionally it reflects an orderliness and precision of technique—as in the hexagonal wax cells of a honeycomb—that simply makes your jaw drop in wonder.

This book is about animal-built structures, but it also is about a question of broader interest in the fields of biology, evolution, and ecology. Are such structures best regarded as external to the animals that build

them, or are they more properly considered parts of the animals themselves? I am an advocate for the latter interpretation, but the argument I present in this book is one with a twist: that animal-built structures are properly considered *organs of physiology*, in principle no different from, and just as much a part of the organism as, the more conventionally defined organs such as kidneys, hearts, lungs, or livers.

The idea that external structures are properly parts of the animals that build them really is not a new idea: the notion of an “extended phenotype,” as Richard Dawkins has so aptly termed it, is well established and has become respectable, if not universally accepted, wisdom in biology. My goal in this book is to bring a physiological perspective to the idea, one which, I hope, complements that of a Darwinian like Richard Dawkins. An evolutionary biologist sees the extended phenotype as the extension of the action of genes beyond the outermost boundaries of an organism and asks how these extended phenotypes aid in the transmission of genes from one generation to the next. A physiologist, however, sees an extended phenotype in terms of mechanism and asks how it works, how it alters the flows of matter, energy, and information through the organism and between the organism and its environment. Although these two perspectives certainly complement one another, I hope to show that they also lead to somewhat different conclusions about the nature of life.

The Two Biologies

The crux of the problem, for both Darwinian and physiologist, is how one perceives the organism. On the face of it, this seems an absurd statement. One of the most obvious features of the living world is that it is composed of organisms, living things that we can hold in our hands, pin down under a microscope slide, give names to, feed and care for, catalog and place in a museum case, admire from afar. In organisms we recognize individuality, intention, purposefulness, function, *beingness*. To entertain *opinions* on what organisms are seems about as rational as disputing the value of π .

Yet that is where biology in the twentieth century has brought us, to a point where it is not at all clear just what organisms are.

We have arrived at this point via two intellectual journeys, resulting, if you will, in two biologies. On one hand, modern biology has relentlessly pursued an understanding of life as a mechanism, as a special case of chemistry, physics, and thermodynamics. For the most part, this mechanistic biology has played out in the study of how cells work, even down to their uttermost details of molecular action. An unintended consequence of this inward focus has been the fading of the organism from relevance: the organism itself has become, at best, an unwelcome distraction from the fascinating cellular and molecular business at hand. It's understandable, really—the mechanistic approach to biology is hardly worth pursuing if it doesn't look for unifying principles of life, fundamentals that do not depend upon whether a living thing is plant, animal, fungus, or bacterium.

At the same time, the twentieth century has seen the emergence of neo-Darwinism as a coherent philosophy of biology. Here, too, the organism has faded from prominence, but for different reasons. To the neo-Darwinist, the organism has become essentially an illusion, a wraith obscuring the “real” biology of the selfish genes that actually run the show. An organism, to the neo-Darwinian, is at most a transient coalition of genes, bound together in a conspiracy to promote the genetic interests of its members.

Although the two biologies have each prospered in their own rights, I think it also fair to say that they have proceeded more or less independently on their respective journeys. I do not mean to say that each of the two biologies has developed in ignorance of the other—far from it. Darwinians are comforted to know, no doubt, how genes really work, what is the chemical basis of heritability and phenotypic variability, and so forth. The molecular biologist may also rest easier knowing that the question of where all life came from is firmly in the good hands of biologists who, like them, are unwilling to admit the arbitrary power of gods as explanatory tools. Nevertheless, mechanistic

biology and evolutionary biology are still, more or less, independent. Let's be honest, now—to what extent, for example, have the quantum-mechanical details of protein folding really informed or challenged the thinking of evolutionary biologists? From the other side, to what extent has, say, the evolution of song dialects in sparrows really changed the course of research in cellular signaling pathways? I think an honest answer to these questions would be “Not very much.” This is a pity, really, because until the two biologies merge, until fundamental questions in one challenge the fundamental assumptions of the other, there can be no claim that we are even approaching a unified science of biology.

Beyond the Obvious Organism

The concept of the extended phenotype offers one way to bridge the divide between the two biologies. Using this bridge, however, requires that we think in yet another way about the organism, as illustrated by the question with which I opened this chapter: are animal-built structures properly things external to the animals that build them, or are they properly parts of the animals themselves? If we believe that animal-built structures are strictly external to their builders, we must posit an outer boundary to the organism, something which delimits it from (to use Boolean language) the NOT-organism. On the face of it, this seems an easy thing to do. The outer integument of the body—whether it be sheets of chitin, or woven socks of collagen, or shells of crystallized calcite or silica—seems to distinguish organisms quite obviously from their surroundings. But are we really justified in delimiting organisms in this way?

Well, yes and no. Certainly, the outer boundary of a living organism is a tangible, obvious thing, a wrapping of some material that keeps the organism contained nicely in a compact package. But it is worth remembering the etymology of the word obvious, which begins with the Latin *obvius* for “in the way” and ends with the modern, and really not very reassuring, usage of “evident without reasoning or observation.” There

is always the possibility that a thing's “obviousness” is literally “in the way,” a mask that prevents us from recognizing the thing for what it is. We must be willing to look past the obvious and ask what might be lurking beyond an organism's “outer” boundary.

Let us begin with a well-worn analogy, the supposed similarity between a turbulent eddy in a flowing stream and an organism. Eddies are familiar features of everyday life: we see one every time we pull the plug in a sink or bathtub. They are also to be found in the turbulent wakes of ships or stationary objects in moving streams, like bridge pilings in a river. Eddies develop when the inertia of a flowing fluid becomes just powerful enough to overcome the viscous forces that keep fluids flowing smoothly. Once an eddy develops, it dissipates this excess inertia as heat, giving rise to smaller eddies, which in turn give rise to still smaller eddies that merge finally into the surrounding fluid.¹

Eddies are popular analogues for organisms because, on a superficial level, they seem to be so very

1. The tendency of turbulent eddies to dissipate their energy by spawning smaller eddies is summarized in a delightful bit of doggerel by L. F. Richardson (1922):

Big whorls have little whorls,
which feed on their velocity;
and little whorls have lesser whorls,
and so on to viscosity.

Richardson's verse itself is a parody of a poem that has become a favorite ditty of entomologists:

Big fleas have little fleas
upon their backs to bite 'em
And little fleas have lesser fleas,
And so, *ad infinitum*.

I am told by R. E. Lewis, the editor of *The Flea Newsletter*, that the original authorship of this poem has been lost. In all likelihood, though, it was inspired by Jonathan Swift, who published this rather more elegant poem in his *On Poetry: A Rhapsody* (1733):

So naturalist observe, a flea
Hath smaller fleas that on him prey;
and these have smaller still to bite 'em;
And so proceed *ad infinitum*.
Thus every poet, in his kind
is bit by him that comes behind.

similar. An eddy is a highly organized entity, seemingly self-contained, whose “purpose” is to dissipate excess inertia as heat. Likewise, an organism takes in energy in the form of light or chemical fuel and uses that energy to construct orderliness, eventually dissipating it as heat. An eddy is a transient phenomenon, persisting only as long as energy is fed into it. So too is an organism—take the fuel away, and a short time later the organism ceases to exist. Of course, one can only stretch an analogy so far before it breaks. One obvious weak point is the seemingly tangible boundary separating an organism from its surroundings. You can take a knife and cut open an organism: you cannot do that with a turbulent eddy.

Now, I confess I have laid a trap for you. If we assert that the boundary of an organism confers on it an identity, a beingness that makes it distinctive from the rest of the world, must we conclude that, because an eddy lacks a distinctive boundary, it cannot have identity?

The Identity of Permanent Eddies

Just downstream from Niagara Falls, there is a permanent eddy in the Niagara River, called simply The Whirlpool (Fig. 1.1). The Whirlpool is located at a dog-leg turn of the river, at an old plunge pool formed when the Falls were located downstream from where they now are. As in all eddies, it is hard to see where The Whirlpool begins or where it ends. Nevertheless, The Whirlpool does seem to have an identity. It has a proper name. Its existence is obvious to anyone who looks over the cliff above the river. Its location can be found on maps. There is even a plaque on the walk along the riverbank that describes it. So, despite there being no obvious boundary separating The Whirlpool from the rest of the Niagara River, it does seem to have an identity. From where, then, does The Whirlpool’s identity come?

The Whirlpool seems to derive its identity not from its *distinctiveness*—that is, in a clear demarcation between Whirlpool and NOT-Whirlpool—but from its



Figure 1.1 The Whirlpool is located downstream from Niagara Falls. Inset: Detail of The Whirlpool, showing general trajectory of flow.

persistence. Like Jupiter’s Great Red Spot, The Whirlpool has persisted long enough for cartographers to put it on their maps and for landscape architects to incorporate it into their park designs. In this sense, The Whirlpool is like an organism: both are persistent in the way an eddy in the wake of a boat is not. So, perhaps we need to explore the analogy a bit further and ask: what is it about organisms and permanent eddies like The Whirlpool that confers on them persistence?

The Whirlpool is a persistent feature of the Niagara River for two reasons. First, the flow of the Niagara River provides a steady source of energy and matter to keep it swirling. Second, the flowing water interacts with specific structural features of the riverbed to channel the flow in a particular way: the dogleg turn

of the river forces the water to change direction as it flows past—water, having mass and inertia, will resist this change—and the old plunge pool provides a venue for the dissipation of the water’s inertia before the water is forced into the sharp turn. Both act together to modify the field of potential energy driving water down the river. The result is The Whirlpool.

For as long as it persists, an organism also modifies energy flowing through it, albeit in a very different way. An organism’s persistence comes from the tangible boundary separating it from its environment. Even though it seems quite solid, an organism’s outermost boundary is actually very permeable, allowing a steady stream of matter and energy to pass continually through it. But, the boundary is not passively permeable, as a sieve would be. Rather, it exerts adaptive control² over the flows of matter and energy across it. Here is the real breakdown in the analogy between a permanent eddy like The Whirlpool and an organism. Turn down the source of potential energy driving The Whirlpool (which the engineers of the New York Power Authority can do by diverting water away from the Falls), and The Whirlpool disappears. Turn down the potential energy driving matter and energy through an organism, and the organism will alter the nature of the boundary separating it from its environment so that it can maintain that flow. It is not the boundary *itself* that makes an organism distinctive, but what that boundary *does*. In other words, the boundary is not a thing, it is a *process*, conferring upon the organism a persistence that endures as long as its boundary can adaptively modify the flows of energy and matter through it.

A curious and paradoxical consequence arises from following the analogy between eddies and organisms

2. I am using *adaptive* in the engineering sense of maintaining a state in the face of changing conditions, like thermostatic control of room temperature. In biology, *adaptation* is a loaded word, in part because it has been used carelessly and recklessly (what animal is not “wonderfully adapted to its environment?”) and in part because it implies a purposefulness that is anathema to many evolutionary biologists.

as far as we have: the obvious and seemingly clearly demarcated boundary separating the organism from its environment disappears. To see why, take the analogy just one step further. An eddy is a consumer of energy, taking in kinetic energy in flowing water and dissipating it as heat. An eddy like The Whirlpool has an indistinct boundary because this inward flow of energy and matter also influences flows elsewhere in the Niagara River. The strength of this influence diminishes with distance: its effects are easy to see close to The Whirlpool’s center but become less distinct the further upstream or downstream you look. Nevertheless, the presence of The Whirlpool leaves an imprint on the flows of matter and energy that extends rather far from the obvious center of its activity. In the jargon of thermodynamics, The Whirlpool is at the center of a field of potential energy that both drives energy or matter through it and that, in turn, is influenced by The Whirlpool’s presence.

Now consider a bizarre question. What would have to happen to make The Whirlpool behave more like a living thing? We have already ruled out adaptive control of the flow of matter and energy across a tangible boundary, like that which occurs in an organism, because turbulent eddies have no tangible boundaries. Suppose, however, that one night, when the New York Power Authority engineers divert water away from the Falls, The Whirlpool effects a change in the shape of the riverbed surrounding it, perhaps by forcing the riverbed downstream to sink in response to the diminished potential energy upstream. In this fanciful scenario, The Whirlpool might persist even in the face of the changing field of potential energy. In other words, if The Whirlpool could persist by adaptively modifying structural features of the environment surrounding it, the distinction between The Whirlpool and an organism—the adaptive control of the flows of energy and mass—would disappear. Could The Whirlpool then fairly be said to be “alive”? Well, that would be stretching the analogy further than even I am comfortable with, but I hope you would agree that we are now in that gray area Mark Twain referred to in his famous

wisecrack about the identity of the author of *The Iliad* and *The Odyssey*: it was either Homer or another blind Greek poet with the same name.

However, it is precisely this “fuzzy” boundary between living and nonliving that is at the crux of the physiology of the extended phenotype. If The Whirlpool can be nudged closer to the realm of the living by conferring upon it the ability to adaptively modify its environment, then what should we think about organisms that do the same? If an organism modifies its environment for adaptive purposes, is it fair to say that in so doing it confers a degree of livingness to its apparently inanimate surroundings? If we agree, just for the sake of argument, that it does, then the boundary between organism and NOT-organism, the boundary that seems so tangible—so obvious—to our senses of vision and touch, dissipates into an indistinct blur, much as a turbulent eddy merges imperceptibly into the water surrounding it.

The Physiology of the Environment

The idea that organisms are integral with the world outside them, like the notion of the extended phenotype, is not new but neither is it an idea that sits comfortably with modern biology, especially neo-Darwinian biology. Consider the simple example of adaptation to some aspect of the environment, say temperature. Generally, organisms seem to have evolved to function well at the prevailing temperatures they normally experience. So, for example, a desert pupfish and an Antarctic ice fish live in very different temperature regimes, yet they each seem to function well in their own environments. Take a pupfish and an icefish and move them to each other’s environments, however, and you will soon have two dead fish. In short, the two species have adapted to function well in their respective, albeit very different environments.

We have a pretty good idea how this process of adaptation works. The conventional story goes something like this: A cohort of individuals exists in an en-

vironment with a certain temperature. Because there will be variation in how well the individuals function at the prevailing temperature, there will be variations in the ability of the members of the cohort to reproduce. To the extent that these functional variations are genetic, the genetic attributes that confer “good” function will translate into high fitness and will be passed on to the next generation. Those that confer “poor” function will not be. The result over many generations will be adaptation, in the evolutionary sense.

What happens to this pretty picture, though, if you suggest that there is no real division between an organism and its environment? The notion of adaptation to the environment thus becomes problematic, because how can an organism adapt to itself? Even more strange, in this view the environment and not just the organism, never mind the genes *in* the organism, can be subject to selection and adaptation. In other words, the environment, and not just the organism, can have fitness. This kind of thinking gives many biologists fits, as is clear in dogmatic statements like the following: “Adaptation *is always* asymmetrical; organisms adapt *to* their environment, *never vice versa*” (emphasis added).³ Nevertheless, the problem of just what the organism is and its proper relationship with the environment is too big (dare I say too obvious?) to be confined by dogma, and biology, fortunately, is returning to this problem in a serious way.

This book is undertaken very much in that spirit, and it is built around the simple idea that structures built by animals are akin to The Whirlpool’s “adaptive modification” of the bed of the Niagara River. By structurally modifying the environment, I will suggest, organisms manipulate and adaptively modify the ways energy and matter flow through the environment. In so doing, they modify the ways energy and matter flow through them. Thus, an animal’s physio-

3. G. C. Williams, “Gaia, nature worship, and biocentric fallacies,” *Quarterly Review of Biology* 67 (1992): 479–486.

logical function is comprised really of two physiologies: the conventionally defined “internal physiology,” governed by structures and devices inside the integumentary boundary of the organism, and an “external physiology,” which results from adaptive modification of the environment.

I have organized my argument for this view into roughly three parts. The first section, comprising Chapters 2 through 4, will build the notion of a physiology that extends outside the conventionally defined boundaries of the organism. Chapter 2 delves into a basic discussion of what physiology is and of the thermodynamic principles governing all physiological function, whether it be internal or external. My overt agenda in that chapter is to convince you that external physiology can exist, that the environment can have physiology. Chapter 3 continues the line of thinking begun in Chapter 2 but focuses more specifically on how external physiology can work. I conclude Chapter 3 with a brief and very general discussion of how, practically, animal-built structures can modify the flows of energy and matter in the environment. Chapter 4, the end of the beginning, explores the apparently spontaneous emergence of orderliness in living systems and outlines a specific example. The interesting feature of this example will be the emergence of physiological function operating in the environment at a scale many times larger than the organisms that generate it. This imposition of orderliness at a large scale, I shall argue, is at the heart of the ability of organisms to be architects and engineers of their environment.

Chapters 5 through 11 represent the biological heart of the book. Each chapter explores how particular animal-built structures function as external organs of physiology. Chapter 5, for example, examines the indivisible link between permanent structures like coral reefs, or the “bodies” of sponges, and the flows of energy and matter in the environment. Chapter 6, on the tunnels dug by invertebrates in marine muds, argues that these structures are devices for tapping one

of the largest potential energy gradients on the planet, the oxidation-reduction potential between our oxygen-rich atmosphere and the reducing muds that are a remnant of the early anoxic Earth. Carrying this discussion to the terrestrial sphere, Chapter 7 considers how earthworms manipulate the physical properties of the soil environment: in so doing, they make the soil an “accessory kidney” that enables them to survive an otherwise forbidding environment. Chapter 8 looks at woven structures, like silken webs of diving spiders and certain types of aquatic cocoons, that serve as accessory lungs and gills. Again, the theme in this chapter is the functioning of an external physiology to create an environment in which the organism’s internal physiology may be maintained. Chapter 9 takes an unusual turn, proposing that leaf galls are animal-built structures that serve to modify leaf microclimates. As part of a rather speculative discussion, I suggest that galls change for the energy budgets of leaves in favor of the parasites infesting them. Chapter 10 presents animal-built structures as communications tools, focusing on the “singing burrows” of mole crickets. Finally, Chapter 11 explores the interaction between structure and physiological function in the nests of social insects, culminating in a discussion of what I regard as the most spectacular animal-built structures on the planet, the large mound nests constructed by certain species of African termites. These mounds, I assert, are not simply houses for the colony but are accessory gas-exchange systems that confer on the termites the power of adaptation to a wide range of environmental conditions. The interesting twist here is that the mounds function at a scale many times larger than the creatures building them. How they create such a system is a fascinating problem in biology, one that cannot be fully understood, I think, without understanding the external physiology that underlies the phenomenon.

For the final section, Chapter 12 returns to the theme of the extended phenotype and the many ways in which animal-built structures illustrate it. I frame

the chapter around a discussion of the *Gaia hypothesis*, which asserts that the Earth is a singular living thing, an entity whose biota are engaged in a massive global physiology. Gaia is, I shall argue, simply the extended phenotype taken to its logical conclusion. I must note,

however, that a physiological approach practiced on a global scale leads one to conclusions about evolution, natural selection, and adaptation that, I think it fair to say, sit uneasily with mainstream evolutionary biology.